Earthworms as Soil Ecosystem Engineers

Patrick Lavelle and Alister V. Spain

Abstract In soils that are the basis of 16 of the 24 ecosystem services recognized by the Millennium Ecosystem Assessment, earthworms play a very important role as soon as conditions allow them to get established. They carry out three types of engineering, physical, community and biochemical. With the energy that they obtain from their mutualistic digestion in association with soil microbial communities, they create a large part of the physical structure of the soil. They create pores of very diverse nature, from the large sub vertical tubular galleries of anecics to porous spaces of diverse shapes and sizes, left between casts deposited in the soil by endogeics. They are also responsible for the aggregation of a significant proportion of soil of the upper horizons, by accumulating casts, in particular those of endogeic communities. The aggregation of several hundred tons of soil per ha in the soils where they are active, greatly influences the provision of hydrological services and C storage in these compact structures. Physical engineering is accompanied by community engineering resulting from the mutualistic mode of digestion which involves a significant selective stimulation of the soil microbial community ingested with soil. In addition, the creation of more or less connected porous spaces affects root penetration and populations of smaller invertebrates which find habitats and nutritional resources there. Finally, the biochemical engineering associated with earthworm activities, the least known of all, allows them, through the release of hormones and other signal molecules produced by the microorganisms under their control, to stimulate the growth of plants and defend them against certain parasites and diseases. Among the various mechanisms involved in biochemical engineering, the modification of the expression of plant genes is the most spectacular. A more in-depth knowledge of these three types of engineering will give stronger arguments to those who want to defend their communities affected by the unsustainable methods of certain agriculture practices and to use them optimally in modern agroecological practices.

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1 Introduction

The Millennium Ecosystem Assessment clearly emphasized the outstanding role of soils in providing ecosystem services (MEA 2005). Sixteen of the 24 services enumerated in this document are directly dependent on soil function (Dominati et al. 2010; Smith et al. 2015; Adhikari and Hartemink 2016). Climate regulation linked to C storage in soils, primary production dependent on nutrient cycling, infiltration and storage of water and its release to water tables and rivers, protection against erosion and flooding, and conservation of biodiversity are among the most cited contributions of soils to the maintenance of sustainable environment conditions. The contribution of soil organisms has been largely emphasized (Lavelle et al. 2006; Barrios 2007; FAO 2020), with special mention of earthworms as key actors of these processes (Blouin et al. 2013).

Soils are also part of the human sustainable development goals of the United Nations (UNDP 2015; Bouma 2014) and considered in the planetary boundary paradigm developed by Rockström et al. (2009). Large reports produced by international agencies give detailed assessments of soil degradation worldwide and expected trends (UNCCD 2016; UNEP 2016; OECD 2019; IPBES 2018).

In this chapter, we first recall the conceptual framework in which the ecological engineering of earthworms fits. We then recall essential features of their interactions with other soil organisms and summarize the various biochemical, community, and physical components of the engineering resulting from these interactions.

2 Conceptual Framework

2.1 Ecosystem Engineering: A Multiscale Key Process of Soil Function

Soils are self-organized systems in which interactions among physical, chemical, and biological processes, across a suite of nested scales, determine the formation and conservation of all basic properties and functions (Lavelle et al. 2016). A suite of five discrete scales has been proposed to describe the general organization in soil ecological processes (Fig. 1). At each scale, organisms interact with the physical elements of the environment and create structures that give the system emergent properties which in turn improve ecosystem functions and ultimately the ability of soils to provide ecosystem services. At the lowest level of resolution of micrometers, microorganisms form colonies (bacteria) and/or networks (fungi) that get associated with soil mineral and organic particles forming a specific type of microaggregates (Tisdall and Oades 1982; Tötsche et al. 2018) or rather large although fragile macroaggregates (Plante) resulting from the entanglement of soil particles in fungal networks.

Although all estimates show that this compartment is responsible for the largest part of soil heterotrophic respiration and overall mineralization activities (Lavelle

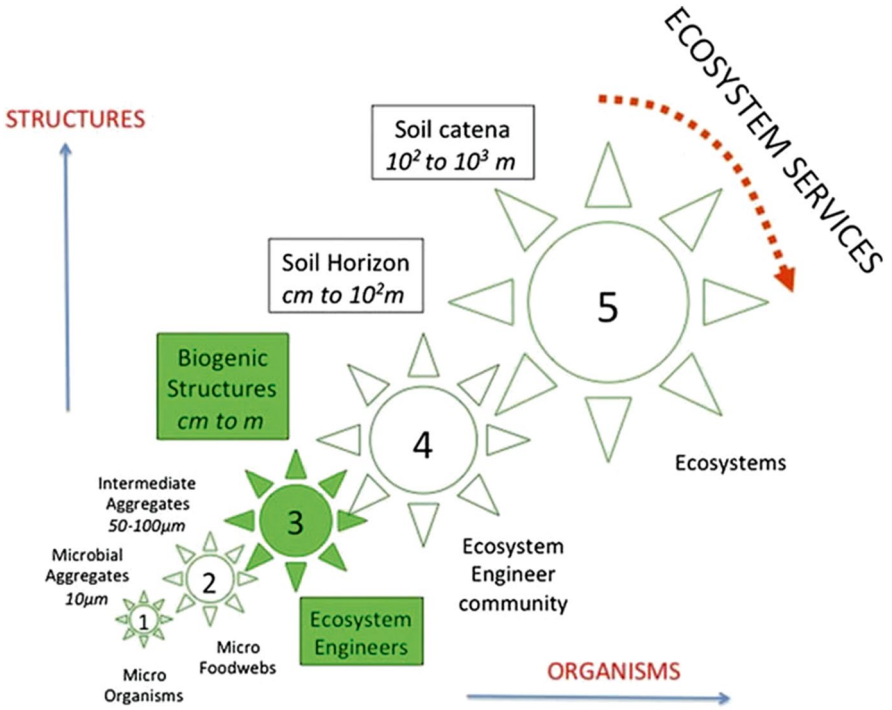

Fig. 1 Soil as a self-organized system of biological entities. Organisms of increasing sizes, from microorganisms to micro-invertebrates (micro-food webs), ecosystem engineers and ecosystems (horizontal axis) create structures of different sizes (vertical axis) and organize soil at different nested scales from 1 (microbial aggregates inhabited by microbial communities) to 5 (landscape viewed as a mosaic of different ecosystems). Most soil-based ecosystem services are perceived and delivered at the landscape (5) scale (Lavelle et al. 2006)

and Spain 2001; Bond-Lamberty et al. 2004; Sacca et al. 2017), microorganisms are inactive great part of the time due to their total (bacteria) or highly limited (fungi) ability to move toward new feeding sources once the one they were feeding on is exhausted. Indeed, at the scale of microbes, organic matter is not a homogeneously distributed source, but rather a set of fragments or local sources (root exudates) dispersed in the volume of mineral soil, randomly in the soil space and/or sporadic in time (Lavelle and Spain 2001).

This inactivity is suggested by visual evidences like dormant bacterial colonies or non-germinated fungal spores and quantified by the great difference observed between estimates of microbial biomass turnover times of several months to more than 1 year and the generation time measured in laboratory tests, when microbes are given optimum conditions for their growth (Spohn et al. 2016).

The composition and activity of microbial communities are then largely dependent on the activities of organisms that operate at larger temporal and spatial scales. The next scale-up (2), that of soil micro-food webs, is observed inpores and aggregate structures around 50 to 100 microns large, formed by the union of microbial

aggregates and other porous and solid elements of the soil. A population of microorganism micro-predators lives in this space where it exerts a very close control of the composition and activity of microbial communities (Hunt et al. 1987; Potapov et al. 2023). Protists, nematodes, and Acari organized in a micro-predator food web are the main actors of self-organized systems at this scale. Although a large part of the soil mineralization activity is claimed to be controlled from these self-organized structures, their existence is determined by the activity of the ecosystem engineers, at the following spatial scale (level 3), of centimeters or more.

Ecosystem engineers have the ability to move the soil, dig galleries and chambers, transport soil at the soil surface or ingest it, and release their casts and pellets that soon become aggregates in the soil structure, of different strengths, morphologies, and compositions, depending on the organism that produced it. The main actors here are roots, social insects (ants and termites), and earthworms plus some Coleoptera, Isopoda, or Diplopoda, occasionally. These ecosystem engineers by concentrating their activities in specific soil microsites and accumulating structures like casts, fecal pellets, soil deposits, galleries, or interaggregate pores create specific functional domains, the rhizosphere around root tips, earthworm, ant, or termites' respective drilosphere, myrmecosphere, or termitosphere (Lavelle 2002).

Roots in their rhizosphere, earthworms, and termites in their guts are responsible for the largest part of priming effects that allow microorganisms to digest organic substrates that had been long considered recalcitrant (Jenkinson et al. 1985; Blagodatskaya and Kuzyakov 2008; Bernard et al. 2012). These priming effects are triggered by the provision of highly energetic substrates that allow microbes to resume their activities and soon restore their enzymatic capabilities and become able to digest any kind of organic resource. Since the selection and activation of microbial communities occur in the gut of invertebrate engineers or in the immediate vicinity of root tips, part of the digestion products is recuperated by the engineer, in an unknown proportion, in what is considered a mutualist digestion system (Lavelle et al. 1995; Trigo et al. 1999). The energy captured this way is used by the engineers for their mechanical activities, moving in the compact soil structure and digging and/or ingesting soil and moving it through the intestinal tract.

At the next level (level 4), in the hierarchy of self-organized systems, that of a soil horizon or profile, communities of ecosystem engineers get organized making soil horizon mosaics of mixed functional domains, defined as the soil volume units associated dominated by the activity of a given engineer.

Finally at the landscape scale (5), soils with different communities get spatially organized in a mosaic of ecosystem types created by topography, changes of soil types along soil catenas, and/or human-driven land uses and plant covers.

Earthworms, as ecosystem engineers, operate at a strategic intermediate scale and are key actors in soil function. Their function as physical engineers has been largely acknowledged in a number of papers and reviews (Lavelle et al. 2006, 2007; Blouin et al. 2013; Bertrand et al. 2015). Less documented is their role as community engineers as they shape microbial, invertebrate, and even plant communities. Finally, their paper as biochemical engineers able to influence genetic expression of plants through complex interactions with microorganisms is a recent and promising field of investigation and application (Blouin 2018) (Fig. 2).

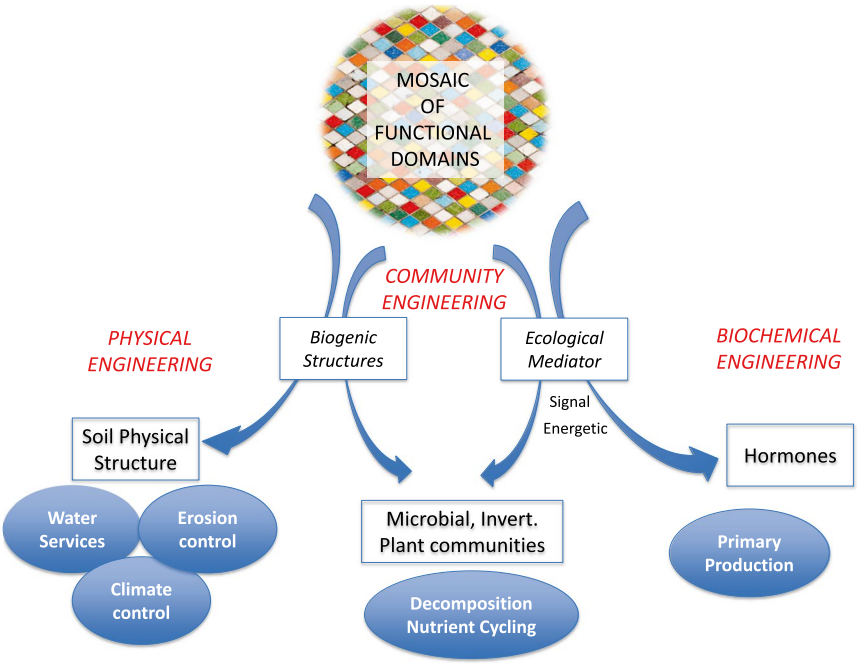

Fig. 2 Soil ecosystem engineers and the delivery of ecosystem services: three different processes (in red). (1) Physical engineering, the organization of soil physical structure and associated ecosystem services. (2) Community engineering, the selection of plant, microbial, and smaller invertebrate communities that determine decomposition and nutrient cycling processes. (3) Biochemical engineering: the release of hormones and signaling molecules that regulate primary production (Lavelle et al. 2016)

2.2 *Where Do Earthworms Get Their Energy From?*

Although the answer seems obvious, behind this apparently naïve question hides a great unknown (Potapov et al. 2022). Soil ecosystem engineers are the only organisms in soils able to move in this compact environment and to arrange it to allow the movement of other organisms and the construction of their habitats. Such a function requires a huge amount of energy. For example, it has been calculated that the African endogeic earthworm *Millsonia anomala* digests daily up to 30 times its own weight of soil when a recently born immature uses 95% of the assimilated energy in respiratory activities, mostly related to the huge effort needed to detach particles from the soil matrix and have them transit in a gut that may be more than 15 cm long in the largest adults (Lavelle 1978).

Depending on their ecological category, earthworms have different feeding behaviors identified by direct observations and confirmed by isotopic analyzes (Martin et al. 1992; Hyodo et al. 2008; Potapov et al. 2019). Epigeics eat leaf litter in the litter system, and anecics drag leaf litter into their burrows and eat them mixed to some soil, sometimes after it has been fermented during some time in an

external rumen digestion strategy (Swift et al. 1979). They are also said to occasionally reingest their own casts, with the same external rumen process. Endogeics feed on mineral soil from the upper few cm of soil that they ingest with little or no selection (mesohumics), enriched with organic matter (polyhumics), for example, feeding in the plant rhizosphere, or just below the litter layer where fecal pellets of primary arthropod or enchytraeids are abundant. Others are so slim that they only ingest the thinner soil fraction rich in clay minerals associated with organic matter.

The real question then comes as follows: what do they really digest? And how much of it?

Earthworm digestion system and specific analyses of digestive enzymes produced in their guts are scarce and, to a certain degree, confusing. Strong enrichment in ^{13}C observed in earthworms tends to support the idea that earthworms feed on microbially processed carbon if not microbial biomass (Potapov et al. 2019). The proponents of the food chain conceptual framework for soil general function then believe that earthworms feed on the microflora of the soil. This vision is opposed to that of the partisans of a mutualist digestion during which the microbes selectively awakened, and activated in the first part of the digestive tract, then carry out the digestion of the organic substrates for the benefit of the microbes and the earthworm, which in this case absorbs a part of the substrates made assimilable (Lattaud et al. 1998). Research provides quite diverse complements that may be summarized in three points:

1. Earthworms generally have weak digestive enzymatic equipments. Cellulase is not produced in gut tissue cultures of some species (*Pontoscolex corethrurus*, *Millsonia anomala*, *Hormogaster elisae*) although *Polypheretima elongata*, *Hyperiodrilus africanus*, or *Dichogaster terrae-nigrae* can produce them (Lattaud et al. 1998; Trigo et al. 1999).
2. Earthworms can digest microorganisms, rather fungi than bacteria. Direct evidence however is only proposed so far for microorganisms that are not present in soil (Shan et al. 2013). On the other hand, decreases in microbial biomass interpreted as signs of a digestion (Aira et al. 2009) may be misleading. A few experiments actually show that the mutualist digestion system that consists in an activation of the ingested soil microflora by intestinal mucus may not be activated when the ingested soil has enough assimilable organic compounds to feed the earthworm (Lavelle et al. 1989).
3. In any case, the assimilation rate (of 8 to 29% as measured by Shan et al. (2013) of a microbial biomass that represents itself a low proportion of the organic matter (less than 5% of the soil organic contents) does not seem to meet the amount of OM actually assimilated, and around 9% in tropical endogeic earthworms (Lavelle 1978) and probably more in species fed more organic substrates. In addition, the amount (5 to 18% of the ingested soil) and energy cost of the intestinal mucus added to the ingested soil do not seem to be justified by a function that would be only lubricating the gut duct.

However, there is no doubt much remains to be discovered in order to fully account for the digestive process of earthworms and a number of intriguing unknowns remain. For example, Pokarzhevskii et al. (1997) show that the amino

acid concentration of earthworms is an order of magnitude, or more, than the average soil concentration. These authors suggest that the source of the amino acids is the microbial biomass and/or that of the microfauna ingested with the soil.

In conclusion, although earthworms may digest some part of the ingested microbial biomass, especially fungal biomass in an opportunistic way, most of the assimilated material seems to be released by the mutualistic digestion system first described by Barois and Lavelle (1986). In this system, the activity of the dormant bacteria ingested with the soil is awakened and stimulated by the secretion of intestinal mucus and the addition of a volume of water and the intense mixing that takes place in the gizzard and the foregut. The dominance of this system over direct digestion by enzymes produced by the earthworm gut wall and/or digestion of living microbial biomass probably varies across ecological categories. One would expect that the mutualist system is all the more active and predominant as the earthworms ingest a soil with low organic matter content and low chemical quality (Lavelle et al. 1995; Trigo et al. 1999).

2.3 *Earthworm Ecological Categories, Ecosystem Engineering, and Ecosystem Services*

There are many ways to be an earthworm, and this diversity must be considered when discussing their impact on soil-borne ecosystem services (Table 1).

Table 1 From earthworms to ecosystem services. A suite of processes that link earthworm adaptive strategies in ecological categories to their feeding processes and the production of stable physical structures through different engineering processes and the emergent properties as ecosystem services

Ecological categories	Feeding processes	Drilosphere structures	Ecosystem engineering	Ecosystem emergent process	Ecosystem services
Epigeic Anecic Polyhumic endogeic Mesohumic endogeic Oligohumic endogeic	Food selection + ingestion	Casts	Biochemical	Decomposition Nutrient + signal molecule release	Nutrient cycling
					Primary production
			Community	Shaping micro-food webs and smaller invert. communities	Biodiversity
	Digestion (host-mediated + mutualist)		Physical	Soil aggregation Carbon storage GHG gas emissions	Climate control
	Comminution and mixing				Erosion control
	Activation selection of soil microbial communities	Pores		Water infiltration	Water services
				Water storage and transfer	Flooding control

Earthworm communities exhibit a continuum of ecological categories that can be ranked according to the relative proportions and qualities of the ingested organic matter and mineral soil and corresponding vertical distribution in the soil profile. Litter-feeding epigeics may ingest up to 100% organic residues, and their main function in the ecosystem is natural composting of fresh leaf litter. Polyhumic endogeics, the soil-living earthworms that ingest a soil rich in organic matter, may feed on concentrations of organic matter at the bottom of the litter system, root litter, and root exudates mixed with soil of the rhizosphere. Rhizophagy has been rarely documented, and experiments show that root litter at different stages of decomposition, in aerobic or anaerobic conditions, is a poor food for the African endogeic *Millsonia anomala* (Lavelle et al. 1989). Isotopic (Spain et al. 1990) or NIR signals (Zangerle et al. 2011) measured on earthworm bodies or casts however indicate feeding links with the rhizosphere system, possibly in the form of root exudates.

At the other end of the continuum, mesohumic and oligohumic endogeics that live on soil from the surface or deeper soil horizons with very low organic contents are mainly physical engineers. They daily ingest several times their own weight of soil, digging their way through the soil and leaving behind pores and casts of different sizes and shapes that comprise their respective drilospheres.

Anecic earthworms that ingest a mixture of leaf litter with mineral soil represent an intermediate situation.

All categories participate in community engineering at shaping the composition and activity of microbial communities, micro-food webs, and other invertebrates and vertebrates. All of them also contribute to the biochemical engineering effect at releasing hormones and other signal molecules with effects on plant growth and gene expression.

Intermediate ecosystem processes and emergent properties like nutrient release, soil macro- and microaggregation, water infiltration, storage in the porous space, and transfer to water tables form the basis of soil-based ecosystem services.

3 Earthworm Ecosystem Engineering

3.1 Biochemical Engineering

Biochemical engineering, the lesser-known mode of ecosystem engineering, profoundly affects the relationship of earthworms with the rest of the soil community. Earthworms produce a number of very specific molecules, here called ecological mediators, that may profoundly affect the activities of other organisms, microorganisms, and plants principally. Biochemical engineering is defined here as the outcome of these interactions, at the ecosystem level.

Ecological mediators of two kinds, energetic and signaling, are released in the drilosphere. Intestinal and cutaneous mucus—apart from their long-alleged function as internal and external lubricants—are key energetic mediators that trigger priming effects on microbial activities.

Signaling molecules produced by plants and soil organisms act as hormones or initiators of signaling pathways leading to the production of phytohormones (Medina-Sauza et al. 2019). These molecules produced in the drilospheres may activate plant growth or influence the expression of plant genes (Blouin et al. 2013).

Intestinal Mucus Extraction with hot water (60 °C) of the water-soluble compounds present in the anterior part of the digestive tract of earthworms produces a transparent yellowish solution which, once freeze-dried, takes on the appearance of a white foam (Martin et al. 1987). Chromatographic analysis of this extract taken in African endogeic earthworms showed three peaks: one between 40 and 60 K d comprised of a glycoprotein; another peak purely proteic around 25Kd, probably comprised of enzymes; and the last peak of low-molecular-weight osides, amino acids, or peptides around 180 d (Fig. 3). This mucus may comprise 5 to 18% of the anterior gut content of endogeic tropical earthworms and up to 25–40% in endogeic earthworms of temperate regions (Fig. 4). Concentrations tend to increase when the organic contents of the ingested soil decrease and/or as temperature decreases, with greater contents in peregrine than endemic species (Lavelle et al. 1995). Such results suggest earthworms invest all the more in mucus addition as low temperature, low contents of organic residues, and/or their relative recalcitrance to mineralization oppose constraints to the mutualistic digestive process (Lavelle et al. 1995). Only present in the anterior part of the earthworm gut, mucus then disappears, and soluble extracts from posterior gut parts present a number of small peaks. They correspond to assimilable organic matter temporarily available before its probable absorption by the gut wall or assimilation by microorganisms.

This mucus represents surprisingly high proportions, from 4 to up to 40% of the dry weight of the fore gut content. The energy represented by the production of this mucus is much higher than what the worm will extract from its digestion of the organic matter of the soil, limited to 3 to 19% of the ingested organic matter. No

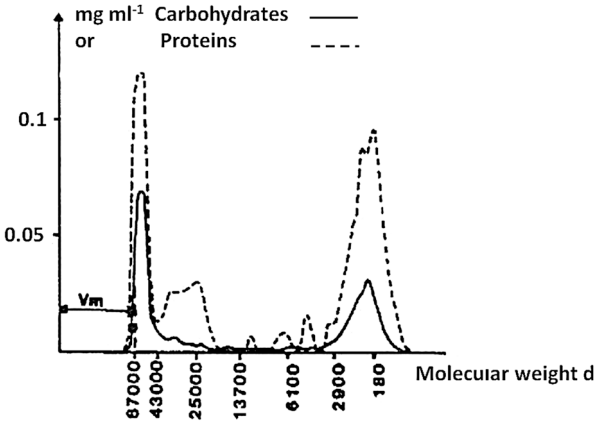

Fig. 3 Gel chromatography of water-soluble extracts from the anterior gut part of *Millsonia anomala* (now renamed *Reginaldia omodeoi*) (Martin et al. 1987)

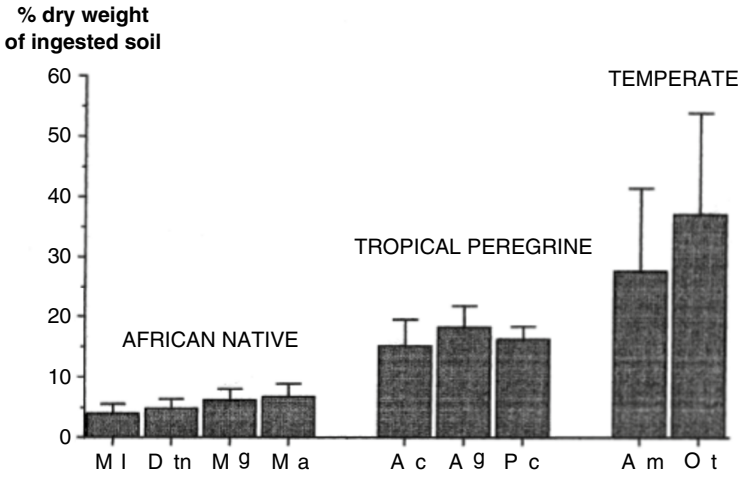

Fig. 4 Proportion of intestinal mucus mixed with the soil ingested by different earthworm species. Ml, *Millsonia lamtoiana*; Dtn, *Dichogaster terrae-nigrae*; Mg, *Millsonia ghanensis*; Ma, *Millsonia anomala*; Ac, *Amynthas corticis*; Ag, *A. gracilis*; Pc, *Pontoscolex corethrurus*; Am, *Allolobophora molleri*; Ot, *Octolasium tyrtaeum* (Lavelle et al. 1995)

longer found in the medium and posterior parts of the digestive tract, the part of the intestinal mucus that has not been metabolized by bacteria is probably re-absorbed.

Cutaneous mucus Cutaneous mucus is a complex mixture of carbohydrates with a high aliphatic/lipid content, acetylated carbohydrates, peptides, and low protein contents (Cortez and Bouché 1987; Shutenko et al. 2020). The amounts produced are not known. They probably vary according to ecological categories and are expected to have been selected by different evolutionary constraints like eliminating excess C from a nutrient poor diet (stoichiometric constraint). Seen from a stoichiometric perspective, the production of intestinal mucus, in addition to the high respiration cost of mechanical activities, is a process that allows eliminating C in excess and adjusts the stoichiometry of organic compounds assimilated during digestion to that of earthworm biomass. Cutaneous mucus is also considered as a mediator in community engineering that attracts Collembola (Salmon and Ponge 2001) and stimulates the development of specific microbial communities on burrow walls where it has been deposited (Loquet et al. 1977; Furlong et al. 2002). Cutaneous mucus also acts as a primer accelerating the turnover of soil organic (Hoang et al. 2016).

Hormones involved in plant growth have been found in earthworm casts of mainly epigeic forms (Medina-Sauza et al. 2019). Production of indole acetic acid, jasmonic acid, salicylic acid, amino-cyclopropane-1-carboxylate (ACC), auxin and auxin-like molecules, ethylene or ethylene precursors, and humic acids observed in drilospheres is mostly considered a result of the activation of specific bacteria, like plant growth-promoting bacteria, in the gut contents and casts of earthworms.

Celomic fluid of various earthworm species has exhibited significant effects as plant growth promoters and pesticidal and antifungal properties (Nadana et al. 2020; Ecimovic et al. 2021).

The outstanding effect of vermicomposts on plant growth is likely due to the release in these products of plant growth-promoting molecules (Pathma and Sakthivel 2012; Zhang et al. 2015).

Biochemical engineering also involves effects on the expression of plant genes, allowed by the release of specific ecological mediators. Modification of the expression of upland rice genes in the presence of earthworm has been reported to render these plants tolerant to plant parasitic nematode attacks (Blouin et al. 2005) Fig. 5. In this case, the overexpression of a leaf lipoxygenase gene and underexpression of a cysteine protease gene, responsible for protein degradation in leaves and their transfer to damaged roots, prevented the inhibition of photosynthesis and allowed a normal survival and growth of the plants. Other signaling molecules produced in drilospheres have the ability to influence the expression of a large number of plant genes (Jana et al. 2010; Puga-Freitas et al. 2012).

Nutrients Another outstanding case of biogeochemical engineering is the release of assimilable nutrients observed in earthworm casts. Fresh casts generally exhibit high concentrations of mineral N and assimilable P (Lavelle and Spain 2001). These nutrients, often produced within reach of growing roots, are available during a limited amount of time, ca. 24 h in the case of fresh casts of *Pontoscolex corethrurus* (Lavelle et al. 1992) before they are either expelled outside the cast and released in the external environment or immobilized in the microbial biomass (Decaëns et al.

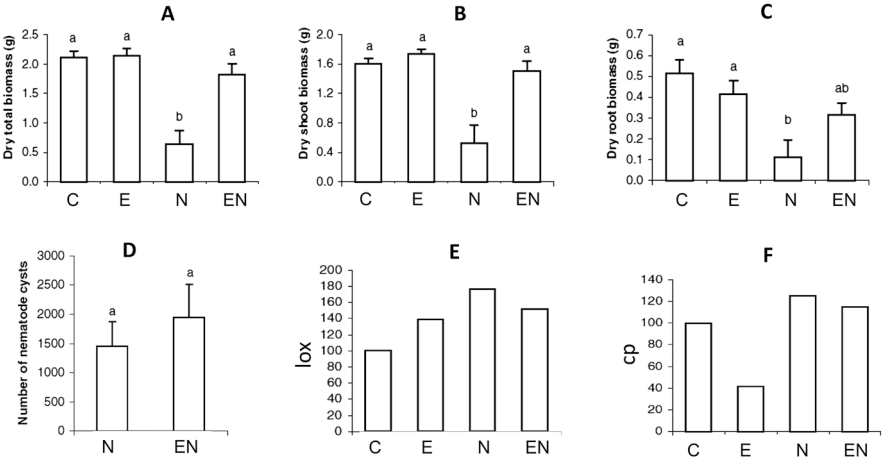

Fig. 5 Rice biomass in different treatments. (**A**) Total dry biomass, (**B**) shoot dry biomass, (**C**) root dry biomass, (**D**) number of nematode cysts per unit of root biomass, (**E**) gene expression (number of transcripts after RT-PCR on total RNAs) of lipoxygenase-1 (lox) and (**F**) cysteine protease (cp). *C* control, *E* earthworms, *N* nematodes, *EN* earthworms and nematodes. Significant differences between means (± 1 SE) are marked by different letters (least square means, Tukey-Kramer test, $P < 0.05$) (Blouin et al. 2005)

1999; Fig. 6). The synchrony between nutrient release and plant uptake realized by this spatiotemporal pattern coincidence prevents nutrient loss to the deeper soil or to the atmosphere (Swift and Anderson 1994). However, an analysis of the mineral contents of dry castings shows higher contents during the lifetime of these structures (Van Groenigen et al. 2019).

An interesting interface with climate regulation is the release of NOx gas, a powerful greenhouse gas, that naturally contributes to the regulation of the earth ozone layer. Claims that earthworms might significantly alter climate via the production of these gases based on the extrapolation of laboratory tests are most probably exaggerated (Lubbers et al. 2013). Excessive earthworm biomasses that create anaerobic conditions favorable to denitrification and the absence of plants to extract mineral N in most experiments have engendered conditions that must be rare if at all possible in nature.

3.2 Community Engineering

Earthworms greatly influence the composition and activities of communities of soil-dwelling microorganisms; micro-, meso-, and macrofauna; and even plants by their feeding and bioturbation activities.

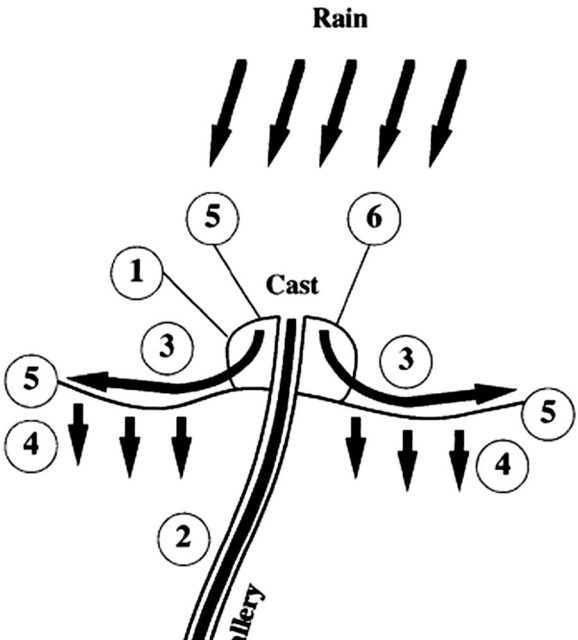

Fig. 6 N dynamics in earthworm casts and the nearby soil. The arrows indicate the direction of water flow, and the numbers refer to a chronological order: (1) high NH4+ release in fresh casts, (2) vertical drainage in the gallery, (3) lateral runoff from the cast and the soil surface, (4) vertical leaching in the soil profile, (5) denitrification plus root and microbial uptake, and (6) N immobilization in dry casts (Decaëns et al. 1999)

3.2.1 Microbial Communities

Earthworm gut represents a very special set of microsites with highly favorable environmental conditions for microbial activities: high water (up to +150% the content of the surrounding soil) and organic contents, neutral pH, and large amounts (4 to 40%) of intestinal mucus added as a primer in the anterior part of the gut (Barois and Lavelle 1986; Trigo et al. 1999; Lavelle and Spain 2001).

Oxygenation varies from microaerophilic to anoxic conditions, while soil progresses from the foregut to the midgut and hindgut parts (Barois and Lavelle 1986; Trigo et al. 1999; Meier et al. 2018). Although this condition may favor microaerobic microorganisms such as denitrifying bacteria, for which earthworm gut is a "transient heaven" (Drake and Horn 2006), soil microorganisms of a wide range of biological profiles may get stimulated during their stay in this succession of highly favorable microenvironments, from the gizzard and crop to fore mid- and hindgut section. The digested soil and/or litter expelled as fresh casts pass through another sequence of states from freshly deposited casts to dry casts and their final belonging to the soil macroaggregate structure (Lavelle et al. 1992; Zangerle et al. 2014).

Analyses of microbial communities in soil, the different parts of earthworm guts, and casts suggest that the specific conditions observed in the different gut parts and casts select and activate alternatively different groups of microorganisms.

While the existence of specific symbiotic bacteria in the earthworm gut is not discarded, there is a general consensus to consider that most microorganisms ingested with soil and litter transit unharmed through the gut and constitute the greatest part of the gut microbiome (Wolter and Scheu 1999; Furlong et al. 2002; Byzov et al. 2009; Medina-Sauza et al. 2019). Although specific bacteria and fungi can be isolated from cleaned gut walls, there is no proof so far that they are symbiotic species of the gut. Part of the microbial community ingested with soil and organic debris is selected and strongly activated (Parle 1963; Brown 1995; Barois and Lavelle 1986; Furlong et al. 2002). Another part seems to be destroyed by midgut intestinal fluid (Byzov et al. 2007). The selected community seems to be composed mostly of generalist bacteria (Huang et al. 2022) that become dominant, and microbial diversity in the gut is lower than in the bulk soil (Aira et al. 2022). A likely consequence of specific activation of different parts of the soil-born microbiota in different sections of the gut and in casts is the large dissimilarities observed in all these sections (Sampedro and Whalen 2007). The negative effect of gut transit on *E. coli* from pig slurry indicated by Monroy et al. (2008) suggests that some bacteria may not find suitable conditions for their survival in earthworm gut contents.

Comparing microbiome of soil, gut contents, and casts of the common endogeic Lumbricidae *Aporrectodea caliginosa*, Aira et al. (2022) found that a large proportion of bacteria identified with 16S rRNA sequencing was unique to each microbiome: 82% in soil, 89% in gut, and 75% in casts (75%). Alpha diversity was maximum during gut transit and decreased in casts. This decrease of overall bacterial richness and diversity in the gut content as compared with the soil has been confirmed in other studies based on different identification techniques (Xia et al. 2022). The effect of earthworm species and soil composition on this selection has also been

noted. In an experiment where endogeic earthworms of the genus *Drawida* were fed a soil enriched with manure (HMs) or manure and lime (HMLs), only 520 OTUs (2.9% of a total of 17,654) were common to all soil and earthworm gut (HMe and HMLe) contents (Fig. 7). Between soil and earthworms of a same treatment, the percentage was 15.7% in the organic-amended HM soil and only 7.8% in the same soil with lime (Zhu et al. 2022) (Fig. 2a). Such differences in the composition of detectable microbial communities were significantly related with expected carbon metabolic functions of the community assessed with PICRUSt2 and FAPROTAX techniques.

In general, soil and organic matter inputs, on the one hand, earthworm species and, on the other hand, may promote different microbial communities. While fungi are commonly identified from earthworm guts and clean gut walls, their participation in the digestive process has not been indicated so far. Microaerophilic to anoxic conditions observed in the earthworm gut seem to limit their activity (Swaby 1950).

3.2.2 Mycorrhizae and Fungal Diseases

While earthworms seem to be closely associated with bacteria in their interactions, interactions with fungi are less well known. Fungi do not seem to participate in the mutualist digestion process, and cases of control by earthworms of fungal plant diseases have been documented. A rather large number of studies on earthworm: arbuscular mycorrhizae interactions show rather diverse outcomes (Reddell and Spain 1991). More recently, in a study by Meng et al. (2021), 60% of records showed enhancement of root colonization in the presence of earthworms and 20%

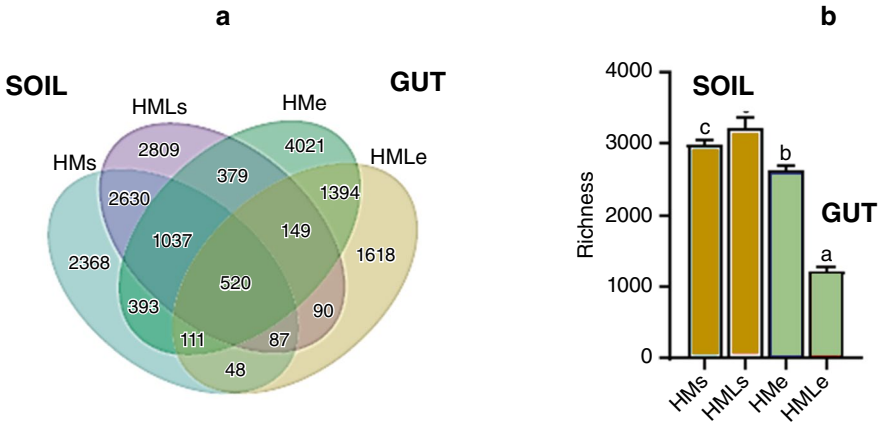

Fig. 7 Common and endemic bacterial taxa in the earthworm gut and adjacent soil. (**a**) Venn diagram showing the number of unique and shared OTUs in the earthworm gut and adjacent soil under manure treatments. (**b**) Richness in soil and gut contents. HMs, control soil with manure treatment; HMLs, control soil with manure and lime treatments; HMe, earthworm gut content fed soil with manure; HMLe, earthworm gut content fed soil with manure and lime

an inhibition, although different effects were observed depending on the ecological categories involved. Epigeic and anecic species generally stimulate root mycorrhizal infection in proportions of 3:1 and 4:1, respectively, while an inverse ratio of 1:2 was observed with endogeic species (Blouin et al. 2013). The higher occurrence of negative cases with endogeic species is attributed to the damage that they do to fungal hyphal networks and fine roots (Gange and Brown 2002) or possible fungal feeding.

Redell and Spain (1991a) reported the presence of putative ectomycorrhizal fungal spores and ectomycorrhizal root fragments in the casts of *Pontoscolex corethrurus* from Australian sites with sclerophyllous vegetation. Spore populations were low, and no concentration effects were noted, as with AM fungi. Few studies of the transmission of the infective propagules of ectomycorrhizal fungi by earthworms have been conducted.

3.2.3 Microfauna Communities of the Soil Micro-food Web

As earthworms ingest several hundred Mg of surface soil each year, and up to 1200 Mg in the humid savannahs of Ivory Coast (Lavelle and Spain 2001), it is likely that all the microsites in which the soil microfauna lives are digested at regular intervals. Earthworms have even been said to be ecosystemivorous, not saprophagous (Pokarzhevskii et al. 1997). Contrasted results have been observed with protozoa. While Rouelle et al. (1985) and Pokarzhevskii et al. (1997) claimed that earthworms might digest them, detailed observations of Monroy et al. (2008) show that they are either unaffected (testate amebae) or stimulated (flagellates and naked amoebae), with different effects of the three epigeic species tested. Astomatous ciliates have been indicated as permanent residents of the gut of anecic earthworms (De Puytorac 1954; Piearce and Phillips 1980). The effects of earthworms on nematodes have been much thoroughly studied with different kinds of results. In general, detritivorous nematodes are not affected by gut transit, while plant parasites often are severely reduced (Loranger-Merciris et al. 2012). While some of them may be directly digested during gut transit, others lose the chemoreceptors that drive them to roots after proteases released by bacteria during gut transit destroyed them. In other cases, eggs hatch in fresh earthworm casts, and larvae become trapped in the compact structure of the cast (Boyer et al. 2013).

3.2.4 Meso- and Macrofauna

Mesofauna and the smallest macroinvertebrates are also influenced by earthworm community engineering. While relationships between microarthropods and epigeics are variable, endogeics have mainly negative effects due to competition for food (Eisenhauer et al. 2010).

Anecics may locally favor microarthropods at providing specific habitats like middens or galleries. Collembola attracted by earthworm casts are often found in

earthworm galleries (Salmon and Ponge 2001; Marinissen and Bok 1988). Earthworm galleries generally have positive effects providing habitat to smaller invertebrates. Higher densities of both Collembola and Acari have been reported in patches of high density of the endogeic *Polypheretima elongata* in pastures of Martinique Island (Loranger et al. 1998). In forest soils of Madagascar, a giant earthworm digs sub-horizontal galleries below the A horizon, all of the same diameter. These galleries seem to serve as ways for the smaller individuals that do not dig galleries (Figs. 8, and 9).

Earthworms may also have indirect negative effects on litter-feeding fauna when large populations of anecics incorporate the greatest part of leaf litter into the soil. This example of amensalism as indicated by Eisenhauer et al. (2010) is observed at the Butte Montceau site near Paris, along a natural gradient of pH created by the outcropping of sand in the upper parts and calcareous sediments on the lower part of a slope (Lavelle and Spain 2001; Fig. 9). With increasing pH, earthworm populations greatly increase, and litter-feeding arthropods decrease as their food resource decreases.

Similar effects on arthropod (Snyder et al. 2009; McCay and Scull 2019) and even woodland salamander populations (Maerz et al. 2009) have been observed when litter accumulation decreases after the invasion of exotic earthworms in North America.

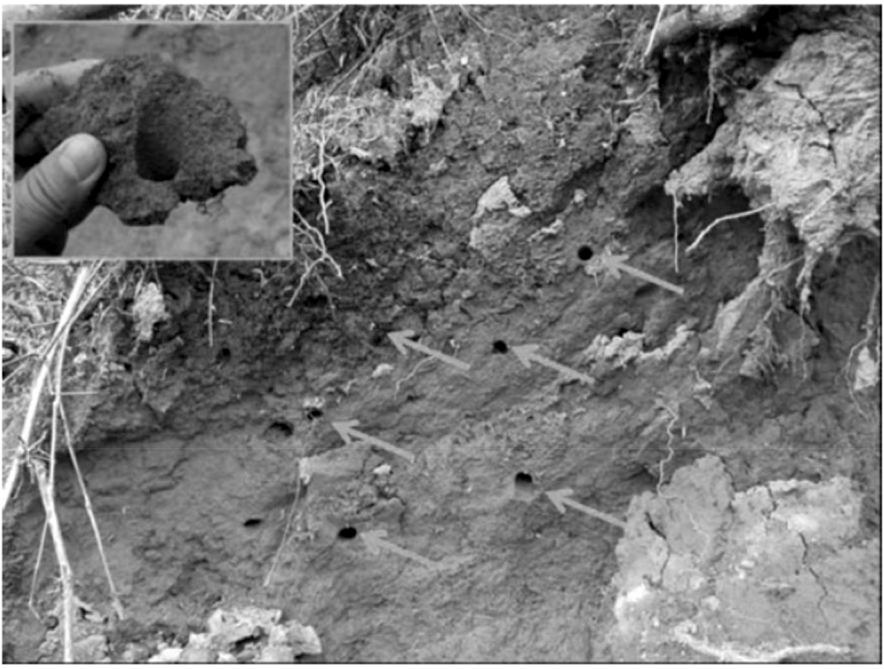

Fig. 8 Large burrow system built by a giant earthworm in the Didy forest (Madagascar). Galleries have the same diameter and orientation. Young worms of the same species and cocoon envelops have been found in these galleries (Photo: P. Lavelle)

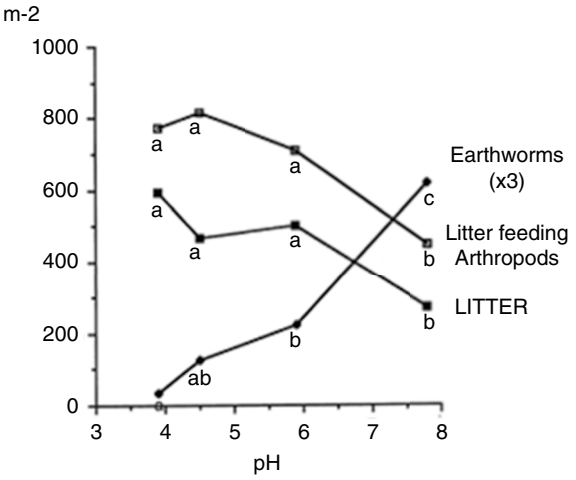

Fig. 9 Correlated changes in soil pH, litter mass, population densities of litter-feeding macroarthropods, and earthworms at Butte Montceau (France) on a hill slope with alternating sand and calcareous bedrock (Lavelle and Spain 2001)

3.2.5 Plant Communities

Earthworms affect plant communities via the selective ingestion and dispersion of seeds and their effects on their germination (Milcu et al. 2006). Seed ingestion by earthworms is common, and gut transit seems to enhance their germination. According to Decaëns et al. (2003) from 0.65% of the seed bank in savanna to 16.7% in old pastures is annually incorporated in earthworm casts in savannahs of the Colombian Orinoquia). At ingesting and egesting viable seeds in their casts, earthworms allow seedlings to germinate in a nutrient-rich medium, protected from seed predators. However, this positive effect may be offset by deep burial of the seeds below emergence depth limits (Regnier et al. 2008) and the digestion of seeds and seedlings observed in *Lumbricus terrestris* (Eisenhauer et al. 2010).

Finally, through a combination of effects on seeds and seedling emergence and differential stimulation effects, earthworms can modify plant communities (Laossi et al. 2009) and suppress weed occurrence in earthworm-corn-associated cropping systems (Li et al. 2020).

3.3 Physical Engineering

Much information has been collected on this effect of endogeic and anecic earthworms, the result of burrowing and casting processes (Blouin et al. 2013; Lavelle et al. 2007).

Although precise data on soil ingestion rates are relatively scarce, some general figures can be proposed. Active endogeic earthworms may daily ingest from 1–2 (*Aporrectodea caliginosa*; Zhang et al) to 20–30 (*Millsonia anomala*, Lavelle 1978) times their own weight of soil. Capowiez et al. (2014) estimated that on average

Allolobophora chlorotica burrowed 22 cm per week. Ingestion rates depend on the relative contents and quality of the organic matter in the ingested soil, temperature, and soil moisture and earthworm size (Lavelle 1975; Lavelle et al. 1989). This means several hundred Mg in most soils where earthworms are present, up to 1200 Mg dry soil annually ingested in an African savanna and transformed into casts, equivalent to several cm of soil, in some cases virtually all the A horizon.

3.3.1 Soil Creep and Erosion

Soil bioturbation and digging by earthworms have significant although contrasted effects as a great diversity of behaviors is observed among species. Casts can either limit surface water runoff (or cause significant erosion, depending on the firmness of their structure and the configuration of the surface, slope, and roughness) (Bertrand et al. 2015). A 75% decrease in runoff on a 40° slope was observed in a Vietnamese soil covered with casts of *Amynthas khami*. Middens of *L. terrestris* have the same effect at increasing soil roughness (Pitkanen and Nuutinen 1998; Le Bayon et al. 2002). Earthworms are also held responsible of part of the biotic soil flux when their casts are carried away by runoff water and accumulate in low-lying areas (Wilkinson et al. 2009). In this process, soil creeping is faster for fine soil particles and decreases with depth (Nye 1955; Nooren et al. 1995).

3.3.2 Earthworm-Induced Aggregation Processes

The ingested soil is first thoroughly dispersed by the intense mixing operated in the gizzard and crop segments and addition to the ingested soil of mucus and water (Shipitalo and Protz 1988; Barois et al. 1993). Digested soil is then defecated in soil or at the soil surface. While anecics tend to deposit a large part of their casts at the soil surface, endogeics deposit very little surface casts (Lavelle 1978; Lavelle and Spain 2001).

A large diversity of cast types has been observed and described (Lavelle and Spain 2001). Two opposite types of casts deposited inside soils can be defined for their either loose or compact structure (Blanchart et al. 1997). Compact casts have round shapes and very low porosities—with bulk densities of up to 1.6 g cm^{-3}. Very fragile and dispersable structures when fresh, they harden tremendously after the first drying event and become highly compact structures covered with a thin, 15-μm-thick crust, made of clay and colloidal molecules with hydrophobic properties (Blanchart et al. 1993; Fig. 10). Inside these casts that have become soil macroaggregates, microaggregates form associating organic matter particles with clay and polysaccharides produced by microorganisms (Fig. 11; Shipitalo and Protz 1989; Six et al. 2000; Bossuyt et al. 2004; Fonte et al. 2007). This protection of organic matter in microaggregates within macroaggregates is a powerful mechanism of C

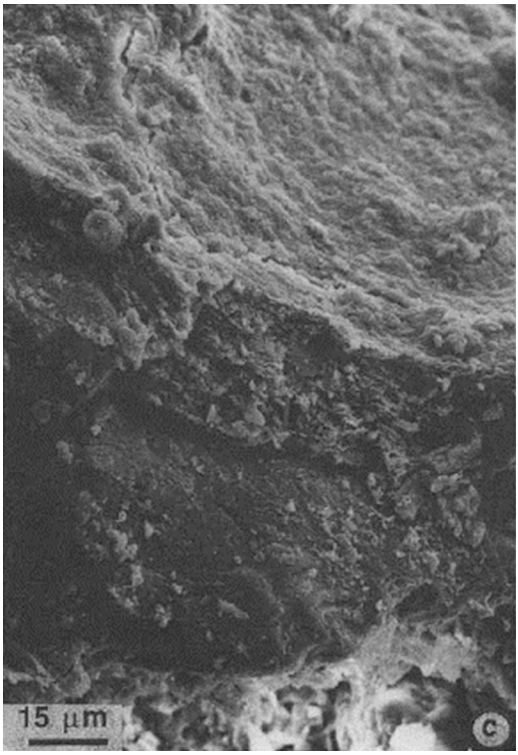

Fig. 10 Scanning electron microscope view of a broken cast of *Millsonia anomala* showing a 15-µm-thick cortex made of fine particles that give the cast a smooth and close aspect (Blanchart et al. 1993)

- Organic matter enriched plasma coagulates
- Resistant organic fragments become plasma encrusted
- Pellets are formed

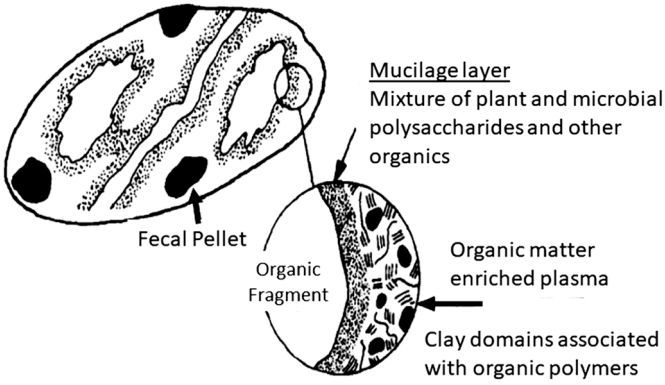
Mucilage layer
Mixture of plant and microbial polysaccharides and other organics
Fecal Pellet
Organic Fragment
Organic matter enriched plasma
Clay domains associated with organic polymers

Fig. 11 Diagrammatic representation of aggregate formation in earthworm casts (Shipitalo and Protz 1989)

storage and protection in soils referred to as "the earthworm C trap" by Zhang et al. (2013). Martin (1991) shows that the loss of C due to the process of ingestion, transit, and digestion of soil organic matter by the endogeic *Millsonia anomala* is compensated for 100 days by the protection induced with the protection in the aggregates. If the aggregate persists beyond this time, the effect of the earthworm becomes a net protection favoring the increase of C stocks in the soil.

These casts may persist for years if no mechanical effect destroys them. In the Lamto savanna, for example, Blanchart et al. (1997) observed virtually no change in soil macroaggregation done by endogeic earthworms after the worms had been removed by flooding soil blocks 20*20 cm and 40 cm deep and replacing the blocks in soil, isolated from further colonization by a metal mesh.

In natural conditions, soil compaction is prevented by a parallel production of lose earthworm casts of the decompacting species or destruction of these compact structures by ant and termites in their digging of galleries and chambers to house their populations and their eventual mushroom cultures. Observation of a soil thin section from an Amazonian oxisol illustrates the participation of both types of macroaggregates to soil physical properties (Barros et al. 2001; Fig. 12). Diversity in soil ecosystem engineers seems to produce soil structures that allow resistance to erosion and C storage in compact macroaggregates, while the accumulation of loose macroaggregated structures, galleries, and interaggregate macro-porosities allows circulation of water and air.

Although earthworms are expected to help maintain stable but perhaps less important carbon stocks in their drilosphere as would occur in their absence, many factors may interfere. Blanchart et al. (2004), for example, show that the effect of earthworms on soil aggregation is maximal in kaolinite soils but negligible compared to the root-aggregating effect in smectite vertisols. Moreover, in soils richer in organic matter, earthworms ingest less soil and therefore produce less macroaggregates.

The overall effect of earthworms on soil aggregation and C storage and conservation in soils is thus the result of an equilibrium between compacting and decompacting effects, all other conditions being equal. The quality of the organic resources and variations in the microstructure of casts according to species and their feeding regimes probably adds their effects. In agricultural soils of Peruvian Amazonia inoculated with the endogeic *Pontoscolex corethrurus*, the proportion of macroaggregates (>1 cm) increased from 25.1 to 32.7% as compared with control with no earthworms, while the proportion of small macroaggregates (<2 cm) decreased from 33.2 to 26.1%, bulk density increased from 1.12 to 1.23 Mg m(−3), and porosity decreased from 58 to 53%. (Alegre et al. 1996; Blanchart et al. 1999).

In other conditions, the overaccumulation of compact casts where the peregrine endogeic species *Pontoscolex corethrurus* is abundant—and decompacting species are absent—may promote severe soil compaction (Chauvel et al. 1999) (Figs. 12 and 13).

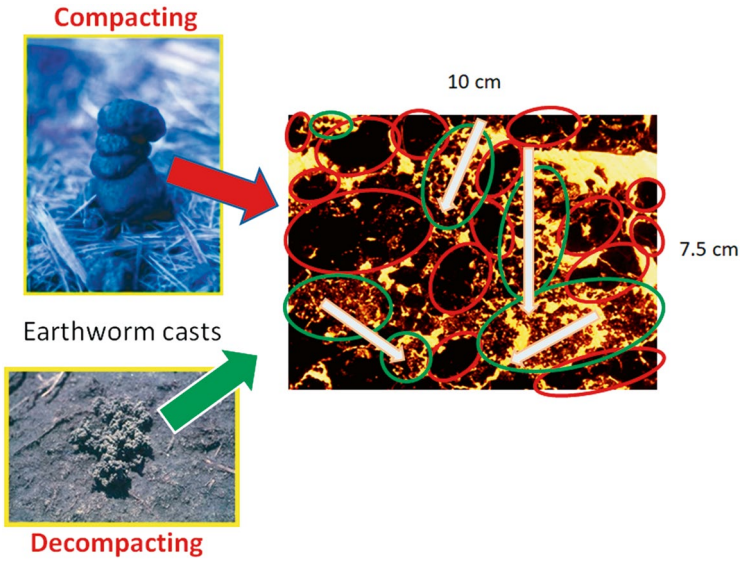

Fig. 12 Distribution of earthworm casts deposited by compacting (red) and decompacting (green) earthworm and other invertebrate species on a thin section of an Amazonian soil. Pale blue arrows suggest water flows in this structure

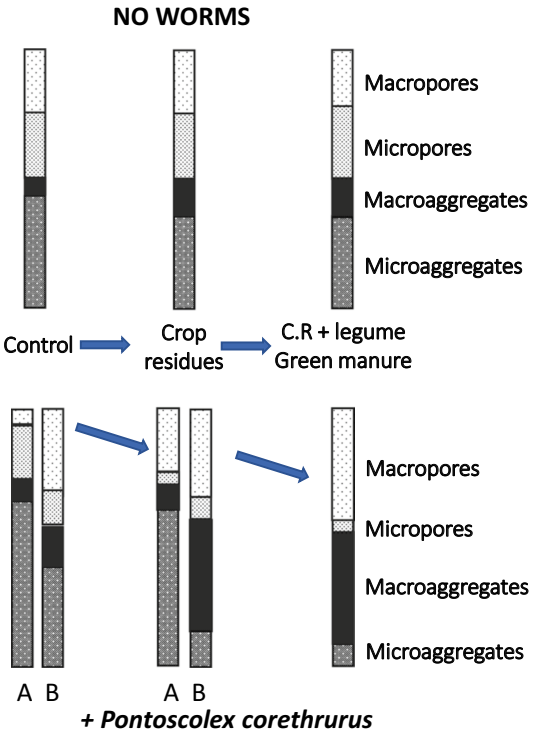

Fig. 13 Effect of earthworm (*P. corethrurus*) introduction and crop residue application on the proportion of aggregates (macroaggregates and microaggregates) and porosity (macro- and microporosity) in thin sections of soil from Yurimaguas (Loreto, Peru). (A) Surface strata (0–1.5 cm) and (B) deeper strata (1.5–4 cm) (Blanchart et al. 1999)

3.3.3 Burrows and Pores

Endogeic and anecic earthworms moving in soil dig galleries and burrows of a great diversity of shapes and sizes, with highly variable effects on soil water infiltration and hydraulic properties.

While anecics build open burrow systems in which water may circulate freely, endogeics excrete the soil they have digested into the gallery they have just dug, partially filling it up and leaving only interaggregated pores of very variable shapes and sizes.

Anecic burrow systems exhibit great variations among species in their depth, orientation, branching, and diameter (Joschko et al. 1993; Jegou et al. 2001; Bastardie et al. 2005). Experiments show that burrow systems are sensitive to local conditions of soil and may reflect competition or commensalism among species.

Anecic burrow systems may be comprised of hundreds of m per m^2. In French pastures, observations varied from 77 to 128 m m^{-3} (Bastardie et al. 2005) to 142–890 m (Kretzschmar 1982). Although this represents total surfaces of 0.7 to 12 m^2, the total volume is equivalent to less than 5%, and only 9 to 43% of this volume was connected to the soil surface (Bastardie et al. 2005). This volume is enough to significantly affect water infiltration, and hydraulic conductivity can be doubled in their presence (Joschko et al. 1993; Bertrand et al. 2015), while increases in infiltration rates of up to 282 mm h-1 per 100 g fw of anecics per m^2 have been measured by Bouché and Al-Addan (1997) in Mediterranean soils.

4 Conclusion

The effects of earthworms as ecosystem engineers have been long studied, with Aristoteles and Darwin as the most famous initial promotors. Their effects as physical engineers have been largely studied and detailed in dozens of papers that describe in great details how they organize soils, creating habitats for a wide range of organisms, from micro to macro, contribute to the storage and conservation of water and organic matter, and interact with roots in this process. The short summary given in this chapter only aims at identifying the major effects and indicates how diverse they are depending on soil types, climates, and ecological strategies. Beyond the wealth of information available, research should now engage toward understanding behaviors that explain the patterns observed. Which part is explained by the genetic heritage, which by interactions with other earthworms of the same or other species, other invertebrates and with plant roots. Communication among earthworms in the compact and supposedly still and silent soil environment is still a total mystery. Do they have territories? Or do they move on a random way? How do the African oligohumic endogeics that live permanently at depths between 30 and 60 cm, and never come to the soil surface, at low densities (sometimes less than one individual per m^2), achieve reproduction? How can they localize a sexual partner at that distance and reach it? Each individual digging its part of a tunnel toward the other one?

Community engineering has benefited enormously of the technical progresses of microbiology. Large amounts of detailed data have been published on the microbiome of the gut and casts of earthworms. However, the vision it gives of the interactions among microorganisms and earthworms is still mostly static, and some results are difficult to interpret. How can microbiomes be so different between the bulk soil, different parts of the gut content, and casts of different ages? Are there autochthonous microbes of the gut, and if it is the case, how can they stay when the gut is traversed by a constant and fast flux of a semi-liquid mixture of water, mineral soil, organic matter, and microorganisms and microfauna ingested with the soil? Another important unknown is the consequence for soil communities of the arrival of peregrine invasive earthworm species. Do they manage to change the microbial community of the soil at ingesting the whole volume of surface soil in a few years? And if so, which consequences does it suppose for native species that developed with a rather specific microbiome, to survive and/or recolonize the soil when suitable environmental conditions have been restored? The example of primary forests in Costa Rica where earthworm community is totally dominated by the invasive *Pontoscolex corethrurus* challenges (Lapied and Lavelle 2003). How can we discard the hypothesis that these forests that were replaced by cropping systems at the Maya time had before the kind of highly diverse and endemic earthworm community as found in the nearby Lacandon forest of Mexico (Fragoso and Lavelle 1987)?

Biochemical engineering is the less known part of earthworm ecosystem engineering. While knowledge of the composition and possible roles of intestinal and cutaneous mucus is available, the physiological bases for their production, metabolism, and possible recuperation in the case of intestinal mucus are not known. Their production has a very energetic cost that needs to be compensated inside the energy budget of earthworms. Energy budgets are only available for a few African earthworms and a single species from temperate areas. Much needs to be done here to better understand the whole system. The other fascinating part of biochemical engineering is the production of signal molecules, hormones, and other molecules involved in signaling pathways that allow earthworms and their drilosphere associates to act upon the expression of genes, in interactions that in the end will benefit the plant.

Beyond such mysteries research should also explore and refine the large conceptual framework and the logics that organizes all these processes. The self-organization theory seems to be a suitable basis to use. Possibly more needs to be imagined to account for all the mysteries of the drilosphere.

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